Influence of temperature on the functional response of *Anisopteromalus calandrae* (Hymenoptera: Pteromalidae), a parasitoid of *Rhyzopertha dominica* (Coleoptera: Bostrichidae)

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Abstract

The functional response of *Anisopteromalus calandrae* (Howard) parasitizing 4th-instar *Rhyzopertha dominica* (F.) on wheat was estimated over a range of temperatures and host densities. A functional response equation was used in which a quadratic component that included temperature was substituted for handling time. The instantaneous search rate increased with increasing temperatures. The maximum rate of parasitization was 13 larvae/24 h at 30°C and 35°C. Handling time was lowest at 30°C and highest at 20°C. The ability of *A. calandrae* to find and parasitize *R. dominica* over a broad range of temperatures makes it a good candidate for natural control of stored grain pests. Published by Elsevier Science Ltd.

Keywords: Functional response; *Anisopteromalus calandrae*; *Rhyzopertha dominica*; Temperature; Host density

1. Introduction

The lesser grain borer, *Rhyzopertha dominica* (F.) is one of the most damaging insect pests of stored grain. Adults feed on both the surface and within the kernels of stored grain, while the larvae develop and feed within the kernels. These insects have been recorded in all parts of the world and are especially prevalent in tropical and subtropical areas (Potter, 1935). *Anisopteromalus calandrae* (Howard) is an ectoparasitic wasp that parasitizes numerous coleopteran hosts (Ghani and Sweetman, 1955). Natural populations of these wasps have been

found in stored maize and wheat (Williams and Floyd, 1971; Arbogast and Mullen, 1987; Dover and Reed, unpublished data). The female wasp parasitizes both the larval and pupal stages of many of the most damaging coleopteran pests of stored cereal and pulses.

The female parasitoid uses certain cues to locate the beetle larvae that develop inside the grain kernels. The wasp may respond to various odors from host products like insect frass. It may also detect host movement or the sound of host feeding as evidenced by antennation of infested grain prior to parasitization. Once the beetle larvae are located, the female uses its ovipositor to drill through the grain surface, paralyzes the larva and lays an egg on it. Host feeding is also common. The female feeds on the host haemolymph to obtain adequate protein for egg maturity. The wasp has a lifetime ovipositional capacity of about 450 eggs (Menon and Dover, unpublished data). Usually one egg is laid per host.

A functional response refers to the change in the parasitization rate of the parasitoid over a range of host densities (Solomon, 1949; Holling, 1968). The assumptions made are that the parasitoid search is random and the host population is distributed at random and is homogenous. There have been limited studies on the effects of temperature on the functional response of parasitoids (Burnett, 1954; Messenger, 1968; Everson, 1980; Mack and Smilowitz, 1982). Some have proposed a general model (Mack and Smilowitz, 1982; Flinn, 1991; Smith, 1994). There have been no reports on the functional responses of *A. calandrae* parasitizing *R. dominica*. The current study describes the functional response of this parasitoid on the final instar of *R. dominica*, over a range of grain temperatures.

2. Materials and methods

Rhyzopertha dominica was reared on whole wheat for several generations in the Stored Products Laboratory, Kansas State University. The cultures were maintained at a temperature of $28 \pm 2°C$ and $65 \pm 5\%$ r.h. *Anisopteromalus calandrae* were obtained from stock cultures from the USDA, SPIRDL, Savannah, GA (now closed). These were maintained on larvae of *R. dominica*, in wheat for several generations at this laboratory. Parasitoids for this experiment were obtained by rearing them on 4th-instar *R. dominica*.

Adult male and female *R. dominica* were allowed to mate and oviposit on cracked wheat in a #30 mesh sieve (595 μm apertures). The sieves were shaken and the eggs collected in the bottom pan. Eggs were transferred to filter paper in a Petri dish and observed for larval hatching. This procedure was repeated every 2 d. The adults on cracked wheat were replaced with fresh adults every 7 d.

Soft white winter wheat was used for the study as these grains could be picked out easily from a mixture of red wheat after the experiment. The germ end of each kernel was pierced to facilitate larval entry. Each grain was placed in a tissue culture well, and one newly hatched *R. dominica* larva was gently transferred to a well containing grain. At 28°C, 4th instars were obtained in about 28 d.

Pint jars (475 ml capacity) containing 330 g of hard red winter wheat at 12% moisture were used for the experiment. The white wheat kernels, infested with 4th instars of *R. dominica*, were mixed with the hard red wheat in the jars to obtain host densities of 1, 2, 4, 8, 16, and 32 larvae per jar.

Newly emerged parasitoids were host-trained by giving them access to a large number of hosts for 3 d. The female wasps were then isolated and deprived of hosts for 24 h before the experiment. One female parasitoid was introduced into each treatment jar and then removed 24 h later. The infested wheat kernels were removed and individually placed in glass vials and observed for parasitoid emergence or beetle emergence. The experiment was carried out at five different temperatures viz., 20°C, 25°C, 30°C, 35°C and 38 ± 2°C and $70 \pm 5\%$ r.h. Each treatment was replicated 10 times.

The type II response is the most common for insect predators and parasitoids. The Hollings Disc Equation, modified by Royama (1971) to give the Random Parasitoid Equation, was used to fit the data:

$$Na = Nt\left\{1 - \exp\left(-\frac{aTPt}{1 + aThNt}\right)\right\}, \tag{1}$$

where Na is the number of hosts parasitized, Nt is the number of hosts available, a is the instantaneous search rate, T is the total time of the experiment, P is the number of parasitoids and Th is the parasitoid handling time. This equation was used to compare the search rates and handling times of the parasitoid across different temperatures. A nonlinear least squares program (Wilkinson, 1989) was used to estimate the coefficients a and Th, using a quasi-Newton method.

A temperature-dependent functional response model developed by Flinn (1991) was also used, in which a quadratic component that included temperature was substituted for handling time. This equation was modified from Royama (1971):

$$Na = Nt\left[1 - \exp\left\{-\frac{aTPt}{1 + a(\beta_0 + \beta_1 X + \beta_2 X^2)Nt}\right\}\right], \tag{2}$$

where X is the temperature in degrees Celsius and all other parameters are as previously described. This four-parameter equation was fitted to the entire data set using a nonlinear least squares program (Wilkinson, 1989) to estimate the coefficients a, β_0, β_1, and β_2.

3. Results and discussion

The Random Parasitoid Equation was fitted separately for each temperature in order to compare the search rate and handling times across different temperatures (Table 1). The efficiency

Table 1
Estimates of instantaneous search rate (a) and handling time (Th) for *Anisopteromalus calandrae* for Royama (1971) type II disk equation for parasitoids

Temp (°C)	Inst. search rate (a) $\pm$ S.E.	Handling time (Th) $\pm$ S.E. (h)	r^2
20	0.020 ± 0.009	12.95 ± 1.72	0.71
25	0.070 ± 0.026	2.47 ± 0.303	0.88
30	0.136 ± 0.053	1.27 ± 0.129	0.96
35	0.504 ± 0.883	1.43 ± 0.155	0.96

of the parasitoid is found to increase with increasing temperature. The instantaneous search rate increased as temperature increased (Table 1) and increased with increasing host density (Fig. 1). At 35°C, the maximum number of larvae parasitized was 15 in a 24-h period. This decreased to a maximum of two larvae parasitized at 20°C. The effect of temperature on handling time is described by Eq. (2). Estimates and standard errors for a, β_0, β_1, and β_2 were 0.0569 ± 0.008, 47.71 ± 0.732, -2.936 ± 0.213, and 0.045 ± 0.00, respectively ($r^2 = 93$; $F = 596.94$; $df = 4$; $P < 0.0001$). We also fitted a six-parameter equation (not shown), where both the search rate and handling time were quadratic functions of temperature. However, since the r^2 value (0.89) was lower than that of the four-parameter equation, we selected Eq. (2) as the best model. At 38°C, there was increased mortality of wasps at lower host densities and so the data were not used to fit the equation. Interestingly, at 38°C more wasps survived at higher host densities than at lower host densities, possibly due to the fact that more hosts were available for host feeding to replenish the fluids lost at high temperatures.

A short handling time increases the time available for search and hence the likelihood of finding additional hosts. The estimated handling time was lowest at 30°C and highest at 20°C (Table 1). An unavoidably long handling time can be compensated for by a long searching period (Hassell, 1978). Adult females of *A. calandrae* can survive as long as 75 d in the presence of hosts, with raisin pulp serving as an additional source of food (Chatterji, 1955). Female parasitoids have been found to survive up to 40 d when provided with a continuous supply of hosts (Menon and Dover, unpublished data). Being a polyphagous parasitoid, it can survive on a variety of internal feeding coleopteran hosts like *Sitophilus oryzae* (L.), *S. zeamais* (Motschulsky) (Press et al., 1984; Williams and Floyd, 1971).

In some parasitoids, more hosts are killed by host feeding than by parasitism (Kidd and Jervis, 1989). However, in the present study, an average of one host was fed upon during the 24-h period. Most of the functional response experiments carried out with *A. calandrae* on different hosts failed to consider this aspect of parasitoid behavior. Smith (1994) and Heong (1982) calculated the rate of parasitism merely on the basis of the number of emerging progeny. Host feeding is an important factor as it not only kills the host but it also provides important nutrients to the parasitoids to sustain their energy and egg production. As discussed previously, this is one of the plausible reasons for the increased survival of the parasitoid at higher than at lower host densities at temperatures of 38°C.

Wheat typically goes into storage at 32°C in Kansas. The search rate of the parasitoid is the highest and the handling time the lowest at temperatures close to this range. During winter storage, temperatures drop to about 20°C and remain at that temperature for some time before it drops to about 15°C. Adult female parasitoids have been found to survive for more than 3 months at temperatures of 15°C, even in the absence of a host (Menon and Dover, unpublished data). At these lower temperatures, the reproductive potential of the host drops to zero.

In summary, the ability of *A. calandrae* to find and parasitize *R. dominica* over a broad range of temperatures makes them good candidates for natural control of stored grain pests in areas like Kansas where temperature fluctuations are frequent. Expert systems already exist for pest management in stored grain (Flinn and Hagstrum, 1990). Flinn and Hagstrum (1995) have developed a simulation model of *Cephalonomia waterstoni* Gahan parasitizing *Cryptolestes ferrugineus* (Stephens), that helps predict host and parasitoid phenology based on grain temperature. The data on the functional response of *A. calandrae* on *R. dominica* at different
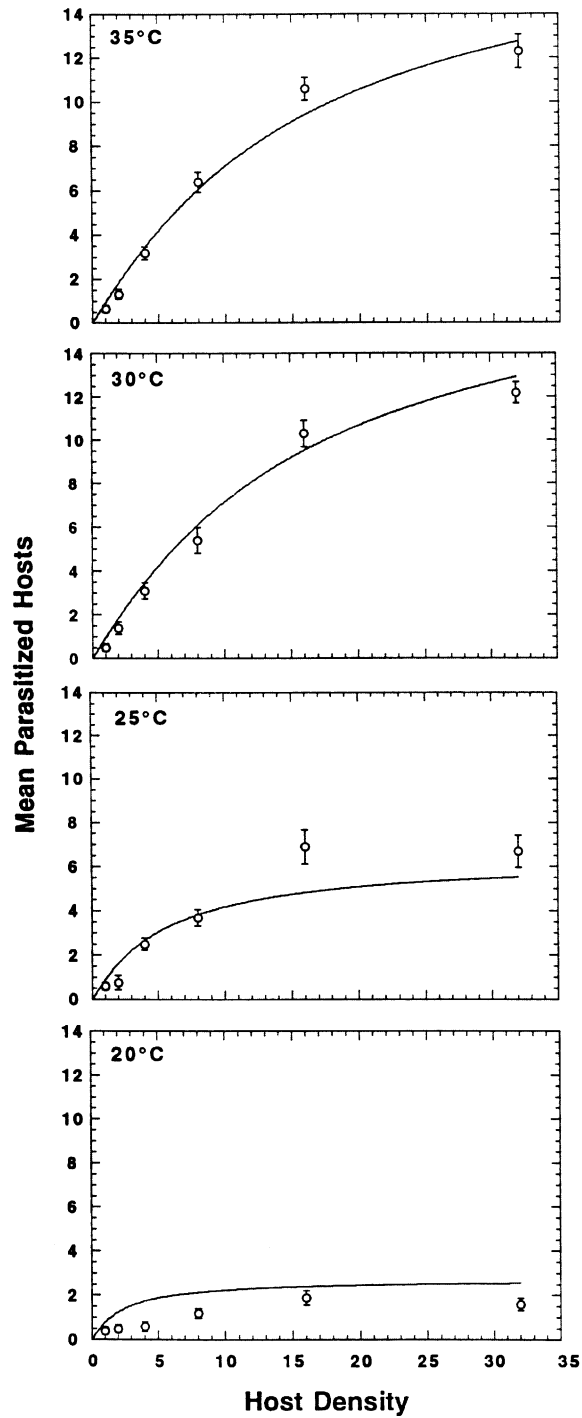
Fig. 1. Functional response of *A. calandrae* parasitizing 4th-instar larvae of *R. dominica* at four different temperatures. Host density is in larvae/330 g of wheat. Vertical bars indicate standard error of the mean.

temperatures could be incorporated into a model to be used in such a system. However, additional studies on the fecundity and development of *A. calandrae* will be needed to develop this model.

Acknowledgements

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